THE PROSAUROPOD DINOSAUR *AZENDOHSAURUS LAAROUSSII* FROM THE UPPER TRIASSIC OF MOROCCO

by FRANÇOIS-XAVIER GAUFFRE

ABSTRACT. *Azendohsaurus laaroussii* was described by Dutuit as an ornithischian dinosaur on the basis of a dentary fragment and two isolated teeth from the Upper Triassic Argana Formation of Morocco. It was subsequently suggested to be a mixture of ornithischian and saurischian remains. Study of further material demonstrates that all the *A. laaroussii* material represents a single valid taxon within the Prosauropoda. However, there is insufficient taxonomic information to place it more precisely and it is considered as Prosauropoda *incertae sedis*. *A. laaroussii* derives from the *Paleorhinus* biochron and is hence Carnian in age and one of the earliest known dinosaurs. Some apomorphic characters attributed to the Ornithischia by Sereno and to the Sauropodomorpha by Gauthier are shown to be invalid. A new synapomorphy of the Prosauropoda is proposed, based on the construction of the maxillary.

A CHARACTERISTIC vertebrate fauna from the important transitional period of the Upper Triassic has been collected from numerous outcrops of the Argana Formation, between Agadir and Marrakech in the western High Atlas mountains of Morocco (Text-fig. 1). These outcrops were discovered and excavated by Dutuit between 1962 and 1969. The material described in this work originated in an outcrop discovered in 1965 and numbered XVI by Dutuit (1976), which is situated in the northern part of the Argana Formation. Lithostratigraphic limits were established by Tixeront (1973) and the outcrops are subdivided into eight levels from the Permian to the Upper Triassic (Text-fig. 2). Outcrop XVI was found at the base of the t5 level, which consists of sandstones and mudstones. Biostratigraphical dating was based on the faunal association of metoposaurs and phytosaurs typical of this period. Outcrop XVI has yielded only one well-preserved specimen, namely a nearly complete phytosaur skull, *Paleorhinus magnoculus* Dutuit, 1977; together with some fragmentary remains of dicynodonts: *Moghreberia nmachouensis* Dutuit, 1988, *Azarifeneria barrati* Dutuit, 1989*a* and *Azarifeneria robustus* Dutuit, 1989*b*; some reptiles including procolophonids (Dutuit, pers. comm.); temnospondyl remains and many tooth-bearing bones and isolated teeth.

Azendohsaurus laaroussii is based upon fragmentary cranial material. Dutuit (1972) described only a fragment of dentary and two isolated teeth. He compared this new taxon only with ornithischians such as *Fabrosaurus*, *Scelidosaurus* and the Heterodontosauridae, and on the basis of this comparison established a new genus and species of ornithischian. This phylogenetic position was immediately challenged by Thulborn (1973, 1974) and Bonaparte (1976), who argued that *A. laaroussii* was a prosauropod dinosaur. Dutuit later revised his position, considering *A. laaroussii* to be firstly a 'pre-ornithischian' (Dutuit 1981), and later to be a prosauropod (Dutuit 1983). Galton (1984, 1985*a*, 1990) and Weishampel (1990) expressed the opinion that the material was from two distinct taxa; the fragment of dentary and one isolated tooth belonging to a prosauropod, and the other isolated tooth belonging to an ornithischian. Additional material, comprising further tooth-bearing bones and teeth, is used to establish the phylogenetic position of *Azendohsaurus* proposed in this study.

The whole material described in this work is deposited in the collections of the Department of

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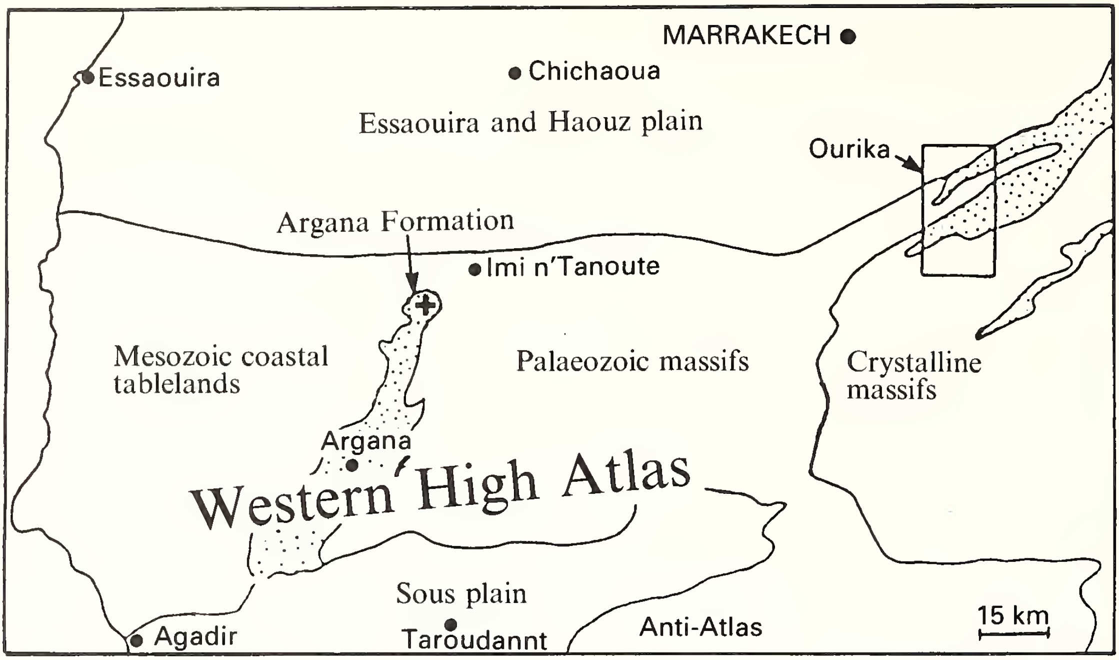

TEXT-FIG. 1. Permian and Triassic outcrops from Argana and Ourika in the High Atlas mountains of Morocco (modified from Dutuit 1976). +, Outcrop XVI.

Lower Lias

------------------------------------Discordance------------------------------------

Upper series

t8: saliferous silts and sands and basalts with doleritic structure

t7: Argana sandstones

t6: pink sandstones

------------------------------------Discordance------------------------------------

t5: sandstones and red clays

t4: silts and sands and sandstones with thin level of conglomerate

t3: conglomerate

------------------------------------Discordance------------------------------------

t2: red sandstones and conglomerate at the top

t1: conglomerate

------------------------------------Discordance------------------------------------

Palaeozoic

TEXT-FIG. 2. Lithostratigraphic section of the Permian and Triassic Argana Formation (from Tixeront 1973).

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STRATIGRAPHY

Biron and Dutuit (1981) ascribed a Carnian age to the t5 level on the basis of similarities observed between t5 of the Argana Formation and F5 of the Ourika Formation (Text-fig. 1). This F5 level was dated directly by palynostratigraphy (Cousminer and Manspeizer 1976; Biron and Courtinat 1982). However, the t5/F5 similarities are of uncertain significance for the following reasons.

(1) The lithology is not strictly identical between t5 and F5, and Biron (1982) admitted that the formations were not necessarily synchronous.

(2) The osteological similarities were based only on very fragmentary material restricted to a 1 m thick calcareous conglomerate, situated at the base of F5 (Biron 1982).

(3) The lower part of the F5 has produced trackways morphologically similar to those from t5, but such ichnological data is of limited value in stratigraphical correlations.

However, one argument is more convincing for assigning a Carnian age to *Azendohsaurus*. Hunt and Lucas (1991) have argued for the existence of a *Paleorhinus* biochron, which can be recognized across much of Late Triassic Pangaea and which can be dated as Carnian in several localities. Since *Paleorhinus* occurs in the outcrop XVI, *Azendohsaurus laaroussii* is considered to be Carnian in age.

SYSTEMATIC PALAEONTOLOGY

Superorder DINOSAURIA Owen, 1842
Order SAURISCHIA Seeley, 1888
Suborder SAUROPODOMORPHA Huene, 1932
Infraorder PROSAUROPODA Huene, 1920
Family *Incertae sedis*
Genus AZENDOHSAURUS Dutuit, 1972

Type species. *Azendohsaurus laaroussii* Dutuit, 1972 from the Upper Triassic of Morocco.

Azendohsaurus laaroussii Dutuit, 1972

Plate 1; Text-figs 3–7

Holotype. MTD XVI 1: a fragment of mandible.

Paratypes. MNHN-ALM 424-5 (MTD XVI 2) and MNHN-ALM 424-4 (MTD XVI 3): two isolated teeth (Text-fig. 7A–B).

Type locality. Outcrop XVI, 1·5 km east of Azendoh, 'Argana corridor', Morocco, coordinates in Lambert system: 161.4/457.5.

Type horizon. Argana Formation, base of t5 level; *Paleorhinus* biochron (Hunt and Lucas 1991), Carnian, Upper Triassic.

Principal referred material. MNHN-ALM 351, a nearly complete left dentary visible in external aspect only (Pl. 1, fig. 1; Text-fig. 3). MNHN-ALM 365-20, a right dentary visible in lingual aspect only and missing the ends (Text-figs 4, 6). Other dentary fragments include MNHN-ALM 353, ALM 365-17 and ALM 365-18. MNHN-ALM 355-3, left maxillary visible in lingual aspect only, and with the posterior region missing and with a damaged dorsal region of the dorsal process (Pl. 1, fig. 2; Text-fig. 5). MNHN-ALM 365-21, isolated right maxillary.

In total, there are fourteen fragments of dentary, including the above, but only four specimens can be examined from both sides. Eight maxillary fragments have been recognized but only one is visible from both sides. Although all jaw fragments bear teeth, the entire dentary row is not preserved on any one specimen. Nine isolated teeth are available.

Diagnosis. A prosauropod dinosaur with the following autapomorphies: neck between crown and root of tooth consistently present; antero-posterior expansion of crown always beginning at its base; prominent longitudinal keel on medial face of maxillary; fossa posterior to dorsal process on medial face of maxillary; entire anterior rim of dentary inclining ventrally, forming angle with dorsal rim of dentary. Other significant characters are: a series of foramina on the medial face of the maxillary, each situated at the base of a tooth; truncate cone-shaped anterior maxillary process with a wide base.

Description

Dentary (Pl. 1, fig. 1; Text-figs 3–4, 6). Although these elements are incomplete, the anterior end of the coronoid protuberance (not a true coronoid process) can be seen in some fragments on the posterodorsal side. The dentaries bear no indication of the external mandibular fenestra. In most fragments, only the outer face is visible, except for four which show the inner face and, in particular, the mandibular symphysis (ALM 353, ALM 365-17, ALM 365-18). The symphysial surface is very irregular and difficult to delimit, but there is no indication of a predentary. The outer surfaces are entirely flat and smooth, with only some foramina situated near the anterior (ALM 351, ALM 353) or along the median portion of the dorsal rim (ALM 365-20). All the dentaries bear teeth, usually between six and eleven. However, teeth have clearly been lost in all specimens and the total number of dentary teeth may have reached seventeen.

Maxillary (Pl. 1, fig. 2; Text-fig. 5). A major portion of the posterior region of the maxillaries is always missing. The available fragments represent two separate regions, the body of the bone and the dorsal process. An anterior process also is present in the continuation of the main body of the bone. The external face of the maxillary is flat and smooth, while the internal face displays a prominent longitudinal keel between the tooth row and the dorsal process, along the entire length of the bone. It also bears a narrow, deep longitudinal fossa situated above the keel, posterior to the dorsal process. A series of ovoid foramina are situated between the tooth row and the longitudinal keel, each one at the base of a tooth. The total number of maxillary teeth is estimated at fifteen to sixteen.

Dentition (Text-fig. 7A–B). The teeth share the following characteristics: a spatulate crown with conical denticles which form an angle of 45° with the rim of the crown, the presence of a neck between the crown and the root, the overlap of the teeth (the anterior rim of each tooth being overlapped laterally by the posterior rim of the preceding tooth), and a thecodont dentition. Most of the teeth can be categorized as one of two types:

Type 1: 8–12 lateral denticles, height/length ratio of 1·5–2, medio-longitudinal keel or ridge present on both faces, edges asymmetrical with different denticle count on anterior and posterior edges, cingula present on both faces. Most but not all dentary teeth are of this type.

Type 2: 4–6 lateral denticles, height/length ratio 1–1·4, medio-longitudinal keels or ridges absent, edges symmetrical with same denticle count on anterior and posterior edges, cingulum present only on outer face. Most but not all maxillary teeth are of this type. There are other teeth which do not conform to either of these types, but show a significant variability of these features with virtually all combinations between the two.

The existence of two different dental morphologies could mean that the fragments derive from two different taxa, but three arguments contradict this. Firstly, on several fragments (ALM 365-20 (Text-figs 4, 6), ALM 352-1, ALM 356, ALM 361) it can be clearly seen that the two tooth types are associated, sometimes with intermediate types. Secondly, several genera of prosauropod dinosaur show significant variation of the dental morphology (e.g. *Sellosaurus* (Galton 1985*b*), *Plateosaurus* (Galton 1985*b*, 1985*c*) and *Massospondylus* (Gow, *et al*. 1990)). Thirdly, the existence of replacement teeth demonstrates that an individual animal can have

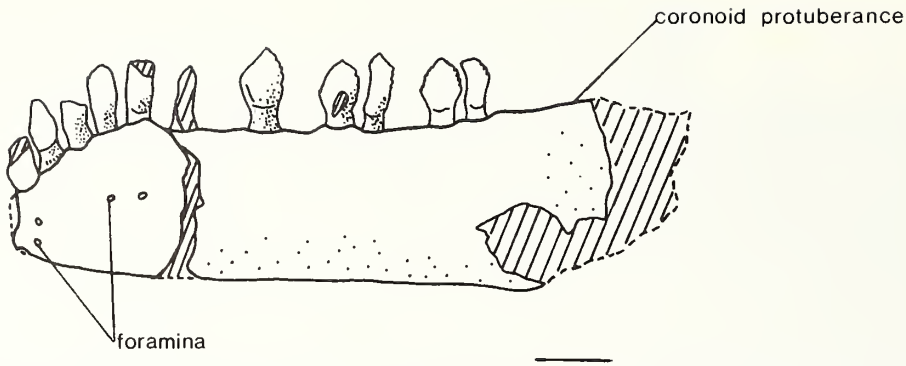
EXPLANATION OF PLATE 1

Figs 1–2. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. 1, MNHN-ALM 351; left dentary in external view, × 1·5. 2, MNHN-ALM 355-3; left maxillary in internal view, × 2·5.

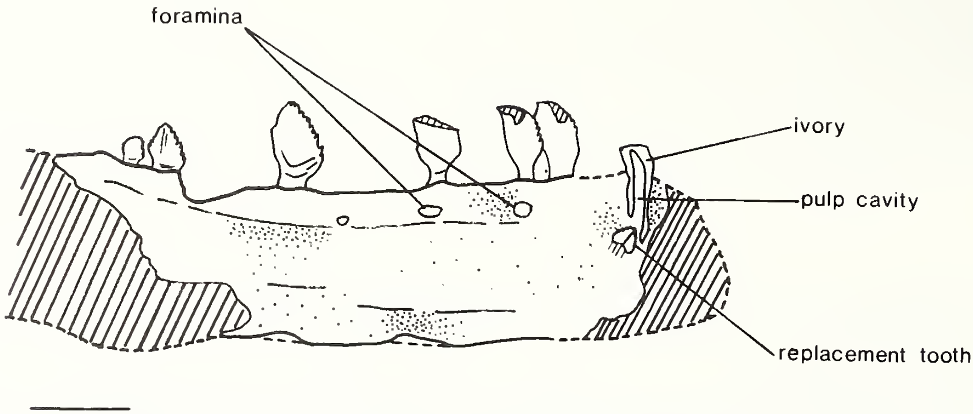
1

2

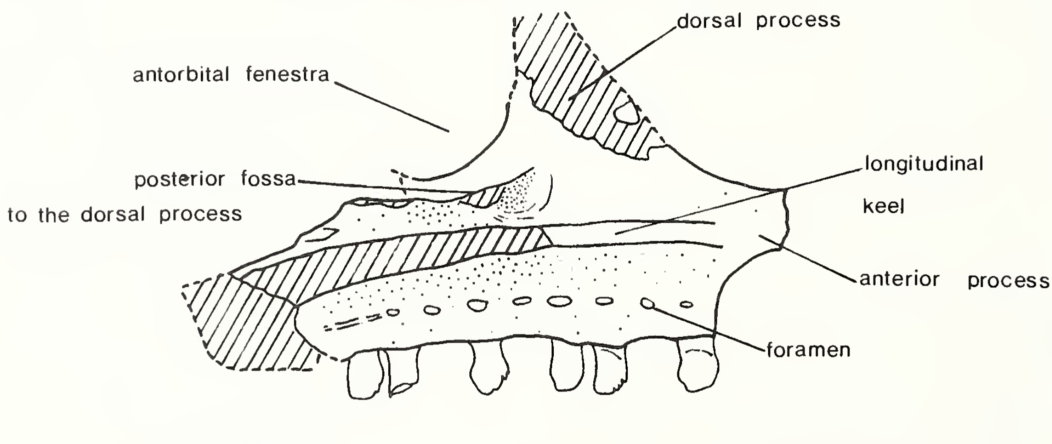
GAUFFRE, *Azendohsaurus*



TEXT-FIG. 3. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. MNHN-ALM 351, left dentary in external view, × 1. Scale bar = 10 mm.



TEXT-FIG. 4. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. MNHN-ALM 365-20, right dentary in external view, × 1·3. Scale bar = 10 mm.



TEXT-FIG. 5. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. MNHN-ALM 355-3, left maxillary in internal view, × 2. Scale bar = 10 mm.

TEXT-FIG. 6. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. MNHN-ALM 365-20, right dentary in external view, ×2. Scale bar = 10 mm.

different tooth morphologies present on the tooth-bearing bones (Gow 1981) and, for example, the number of denticles changes between successive dental generations (Gow *et al.* 1990).

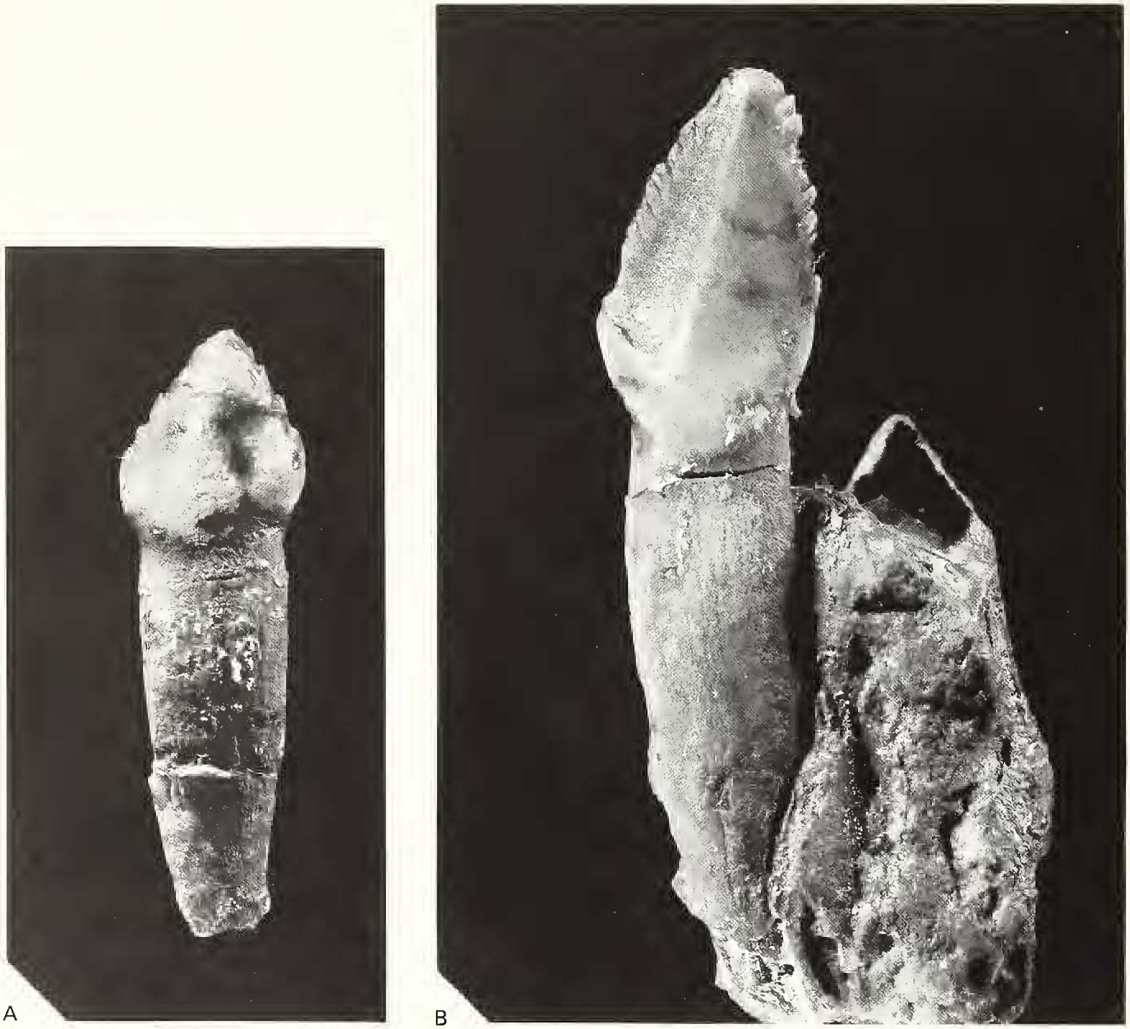
In conclusion, all the fragments attributed to *A. laaroussii* can be assigned to a single genus and species.

SYSTEMATIC POSITION

In order to place *Azendohsaurus laaroussii* systematically, it is necessary to search for derived characters or apomorphies defining dinosaurian taxa, based on the teeth and tooth-bearing bones. Benton (1984, 1990), Gauthier (1986), Sereno (1986), Novas (1992), Sereno, Forster, Rogers and Monetta (1993) have provided cladistic analyses leading to definition of the Dinosauria and its major subgroups. However, they found few fundamental diagnostic characters based on the skull. Novas (1992) did not list any cranial apomorphy for the Dinosauria. Gauthier (1986) and Benton (1990) mentioned only the elongate vomers reaching caudally at least to the level of the antorbital fenestra, and Sereno *et al.* (1993) mentioned five cranial apomorphies, none of which concern the maxillary and dentary. These characters thus cannot be used here, and consequently no character can be used to assign *A. laaroussii* to the Dinosauria as defined at its basal node. However, a general comparison with the non-dinosaurian groups of this period suggests that *A. laaroussii* belongs to this group, and the morphology of the teeth closely resembles that of prosauropods and ornithischians.

A limitation on further analysis is that the Upper Triassic and Early Jurassic Ornithischia are known from only a few well-characterized taxa, namely *Fabrosaurus* (*Lesothosaurus* is regarded as a junior synonym following Thulborn 1992), *Scelidosaurus* and *Heterodontosaurus*, most other genera being based on more fragmentary remains.

Defining apomorphies utilizing the teeth and tooth-bearing bones are claimed for the Ornithischia (six listed by Sereno 1984, 1986) and the Sauropodomorpha (two listed by Gauthier 1986), but none are reported for the Prosauropoda (Sereno 1989; Galton 1990). These and other characters (Paul 1984, Galton 1985*a*) are listed and discussed below.



TEXT-FIG. 7. *Azendohsaurus laaroussii* Dutuit; t5 level; Azendoh, Morocco. Paratypes. (A) MNHN-ALM 424-4, isolated tooth in external aspect. (B) MNHN-ALM 424-5, isolated tooth. Both ×6. Scale bars = 5 mm.

Dental characters

(1) Recurvature absent in maxillary and dentary teeth. An ornithischian apomorphy according to Sereno (1986), but a similar condition occurs in prosauropods.

(2) Overlap of adjacent crowns in maxillary and dentary teeth. An ornithischian apomorphy according to Sereno (1986), but a similar condition occurs in prosauropods.

(3) Well-defined neck separating crown from root. An ornithischian apomorphy according to Sereno (1986), but a similar condition occurs in some prosauropods (*Sellosaurus* Galton 1985*b*, *Thecodontosaurus* Kermack 1984, *Massospondylus* Gow *et al.* 1990).

(4) Low and triangular crowns in lateral view. An ornithischian apomorphy according to Sereno (1986). A high crown is the widespread condition in prosauropods, but *Lufengosaurus* (Young 1947) bears low triangular crowns, and other prosauropods show quite fundamental variation in crown size on the tooth rows (Kermack 1984; Galton 1985*a*, 1985*b*; Gow *et al.* 1990). In contrast, the

ornithischians *Heterodontosaurus* (Charig and Crompton 1974) and *Pisanosaurus* (Bonaparte 1976) have high crowns which are rather rectangular in shape.

(5) Maximum tooth size attained near the central or posterior region of the maxillary and dentary tooth rows. An ornithischian apomorphy according to Sereno (1986), and not contradicted here.

(6) Buccal emargination on maxillary (Genasauria apomorphy, Sereno 1986), slight emargination is visible in *Fabrosaurus* (Sereno 1991).

(7) Lanceolate teeth with coarsely serrated crowns. A sauropodomorph apomorphy according to Gauthier (1986), but invalid as most sauropods lack serrated crowns (see also character 4).

(8) Maximum tooth size at a quarter to a third of the length from the anterior of the maxillary and dentary rows. A sauropodomorph apomomorphy according to Gauthier (1986), and not contradicted here.

According to Galton (1985*a*) and Sereno (1986, 1991), the following dental characters are distinct in ornithischians and prosauropods.

(9) Wear surfaces in most ornithischians (except *Fabrosaurus*), but not in most prosauropods (except yunnanosaurids). All ornithischians show wear surfaces, including *Fabrosaurus* (Sereno 1991), and contrary to Galton (1990), I consider that only yunnanosaurids show clear wear on surfaces with a very typical dental morphology, namely an asymmetrical crown with an apex on the inner side.

(10) Symmetry of the tooth edges in ornithischians but not in prosauropods. However, in *Fabrosaurus* there is slight asymmetry of the anterior and posterior edges, and a different number of denticles on these edges in all teeth.

(11) Number of denticles, low in ornithischians and high in prosauropods. However, the number of denticles in some prosauropods is small: five to seven on some *Massospondylus* teeth (Crompton and Attridge 1986), and the number may vary within and between genera (Gow *et al.* 1990).

(12) A cingulum is present in ornithischians but is relatively uncommon in prosauropods. There is little published information available on the cingulum, and it is not discussed further.

Osteological characters

(13) Ventral margin of antorbital fossa parallels maxillary tooth row. An ornithischian apomorphy according to Sereno (1986), but a similar condition occurs in the prosauropods *Lufengosaurus*, *Massospondylus*, *Plateosaurus* and *Anchisaurus* (Galton 1990).

(14) A predentary is an ornithischian apomorphy (Sereno 1986).

(15) A spout-shaped mandibular symphysis is an apomorphy for Genasauria (Sereno 1986). It is present in *Fabrosaurus* (Sereno 1991).

(16) In prosauropods, the dentary is curved downwards (Paul 1984). However, ventral curvature is absent in *Anchisaurus* (Galton 1976), juvenile *Massospondylus* and *Tawasaurus* (Sereno 1991) and weakly developed in *Coloradisaurus*, *Thecodontosaurus* juvenile and *Sellosaurus*.

(17) Numerous small foramina in prosauropods, in contrast to few large foramina in ornithischians (Paul 1984). In the ornithischian *Fabrosaurus* there are numerous small foramina (eight to nine on the maxillary) as found in some prosauropods (*Massospondylus* Gow *et al.* 1990). Conversely, there can be low numbers of foramina in other prosauropod genera (e.g. *Plateosaurus* Galton 1985*b*, 1985*c*).

Personal observation permits the addition of a further character which I propose as an apomorphy for the Prosauropoda, using respectively sauropods and ornithischians as outgroups.

(18) The dorsal process of the maxillary is fully individualized and its base is situated in the anterior half of the bone, usually in the anterior third, but never in the posterior half.

Of the above eighteen characters, eleven (1–4, 7, 10–13, 16–17) are sufficiently ambiguous in their distribution that they do not permit *Azendohsaurus laaroussii* to be placed in the dinosaur phylogeny, and one (15) is not visible in *Azendohsaurus*. However, six characters appear to stand as valid apomorphies defining major groups, namely character 8 defining the Sauropodomorpha, character 18 defining the Prosauropoda, characters 5, 6 and 14 defining the Ornithischia, and character 9 defining the Ornithischia but convergently present in the Yunnanosauridae.

As *Azendohsaurus* possesses characters 8 and 18, and lacks characters 5, 6, 9 and 14, it can be argued to be a non-yunnanosaurid prosauropod dinosaur.

CONCLUSION

The material of *Azendohsaurus laaroussii* is consistent with attribution to a single genus and species of dinosaur. It possesses the following taxonomically significant characters: the dorsal process of the maxillary is well individualized with its base situated in the anterior half of the bone (prosauropod); there are no wear surfaces on the teeth (non-yunnanosaurid prosauropod); the maximum height of the dentition is reached between the anterior quarter and the anterior third of the tooth row (sauropodomorph); there is no evidence of a predentary (non-ornithischian); there is no buccal emargination on the maxillary (non-ornithischian). In conclusion, *Azendohsaurus laaroussii* is a member of the Prosauropoda, but is not determinate within that infraorder, beyond the fact that it is not a yunnanosaurid. It appears to be of Carnian age and is thus not only one of the earliest prosauropods but also one of the earliest dinosaurs.

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REFERENCES

BENTON, M. J. 1984. Fossil reptiles of the German Late Triassic and the origin of dinosaurs. 13–18. *In* REIF, W. E. and WESTPHAL, F. (eds). *Third symposium on Mesozoic terrestrial ecosystems.* Attempto Verlag, Tübingen, 259 pp.

—— 1990. Origin and interrelationships of dinosaurs. 11–30. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria.* University of California Press, Berkeley, Los Angeles, Oxford, 733 pp.

BIRON, P.-E. 1982. *Le Permo-Trias de la région de l'Ourika* (*Haut-Atlas de Marrakech, Maroc*). Thèse de 3ème cycle de géologie appliquée. Université scientifique et médicale de Grenoble, 2 tomes. 170 pp.

—— and COURTINAT, B. 1982. Contribution palynologique à la connaissance du Trias du Haut-Atlas de Marrakech, Maroc. *Geobios*, **15**, 231–235.

—— and DUTUIT, J. M. 1981. Figurations sédimentaires et traces d'activité au sol dans le Trias de la formation d'Argana et de l'Ourika (Maroc). *Bulletin du Muséum National d'Histoire Naturelle, 4ème série*, **3** (*section C, 4*), 339–427.

BONAPARTE, J. F. 1976. *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. *Journal of Paleontology*, **50**, 808–820.

CHARIG, A. J. and CROMPTON, A. W. 1974. The alleged synonymy of *Lycorhinus* and *Heterodontosaurus*. *Annals of the South African Museum*, **64**, 167–189.

CHATTERJEE, S. 1984. A new ornithischian dinosaur from the Triassic of North America. *Naturwissenschaften*, **71**, 630–631.

COUSMINER, H. L. and MANSPEIZER, W. 1976. Triassic pollen date Moroccan High Atlas and the incipient rifting of Pangea as Middle Carnian. *Science*, **191**, 943–945.

CROMPTON, A. W. and ATTRIDGE, J. 1986. Masticatory apparatus of the larger herbivores during the Late Triassic and early Jurassic times. 223–236. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs.* Cambridge University Press, 378 pp.

DUTUIT, J. M. 1972. Découverte d'un dinosaure ornithischien dans le Trias supérieur de l'Atlas occidental marocain. *Comptes Rendus de l'Académie des Sciences*, **275** (série D), 2841–2844.

—— 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers Stégocéphales recueillis dans le couloir d'Argana. *Mémoire du Muséum National d'Histoire Naturelle*, (*série C*), **36**, 253 pp.

—— 1977. *Paleorhinus magnoculus*, Phytosaure du Trias supérieur de l'Atlas marocain. *Géologie méditerranéenne*, Annales de l'Université de Provence, tome IV, **3**, 255–268.

—— 1988. Ostéologie crânienne et ses enseignements, apports géologique et paléoécologique, de *Moghreberia nmachouensis*, Dicynodonte (Reptilia, Therapsida) du Trias supérieur marocain. *Bulletin du Muséum National d'Histoire Naturelle*, 4ème série, **10** (3), 227–285.

—— 1989*a*. *Azarifeneria barrati*, un deuxième genre de Dicynodonte du Trias supérieur marocain. *Comptes Rendus de l'Académie des Sciences*, série II, **309**, 303–306.

—— 1989*b*. Confirmation des affinités entre Trias supérieurs marocain et sud-américain: découverte d'un troisième Dicynodonte (Reptilia, Therapsida), *Azarifeneria robustus*, n. sp., de la formation d'Argana (Atlas occidental). *Comptes Rendus de l'Académie des Sciences*, série II, **309**, 1267–1270.

GALTON, P. M. 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla*, **169**, 98 pp.

—— 1985*a*. Diet of prosauropod dinosaurs from the Late Triassic and Early Jurassic. *Lethaia*, **18**, 105–123.

—— 1985*b*. Cranial anatomy of the prosauropod dinosaur *Sellosaurus gracilis*, from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg, West Germany. *Stuttgarter Beiträge zur Naturkunde*, **118** (B), 1–39.

—— 1985*c*. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. *Geologica et Palaeontologica*, **19**, 119–159.

—— 1990. Basal Sauropodomorpha–Prosauropoda. 320–344. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, Los Angeles, Oxford, 733 pp.

GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. 1–55. *In* PADIAN, K. (ed). *The origin of birds and evolution of flight*. California Academy of Sciences, Memoir 8, 98 pp.

GOW, C. E. 1981. Taxonomy of the Fabrosauridae (Reptilia, Ornithischia) and the *Lesothosaurus* myth. *South African Journal of Science*, **77**, 43.

—— KITCHING, J. W. and RAATH, M. A. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for palaeontological research. *Palaeontologica Africana*, **27**, 45–58.

HUENE, F. von. 1920. Bemerkungen zur systematik und stammesgeschichte einiger reptilien. *Zeitschrift für Induktive Abstammungs und Vererbungslehre*, **24**, 162–166.

—— 1932. Die fossile reptil-ordnung Saurischia, ihre entwicklung und geschichte. *Monographien zur Geologie und Paleontologie*, **4** (ser. 1), 1–361.

KERMACK, D. 1984. New prosauropod material from South Wales. *Zoological Journal of the Linnean Society*, **82**, 101–117.

NOVAS, F. E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology*, **35**, 51–62.

OWEN, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Science*, **2**, 60–204.

PADIAN, K. 1990. The ornithischian form *Revueltosaurus* from the petrified forest of Arizona (late Triassic: Chinle Formation). *Journal of Vertebrate Paleontology*, **10**, 268–269.

PAUL, G. S. 1984. The stegosaurian dinosaurs: relics of the prosauropod-ornithischian transition? *Journal of Vertebrate Paleontology*, **4**, 507–515.

SEELEY, H. G. 1888. The classification of the Dinosauria. *Report of the British Association for the Advancement of Science*, **57**, 698–699.

SERENO, P. C. 1984. The phylogeny of the Ornithischia, a reappraisal. 219–222. *In* REIF, W. E. and WESTPHAL, F. (eds). *Third symposium on Mesozoic terrestrial ecosystems*. Attempto Verlag Tübingen, 259 pp.

—— 1986. Phylogeny of the bird-hipped dinosaurs (order Ornithischia). *National Geographic Research*, **2**, 234–256.

—— 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. *Journal of Vertebrate Paleontology*, **9** (supplement 3), 38A.

—— 1991. *Lesothosaurus*, "Fabrosaurids", and the early evolution of Ornithischia. *Journal of Vertebrate Paleontology*, **11**, 168–197.

—— FORSTER, C. A., ROGERS, R. R. and MONETTA, A. M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature*, **361**, 64–66.

THULBORN, R. A. 1973. Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. *Serviços Geológicos de Portugal*, *Memoria*, **22**, 89–134.

—— 1974. A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic Red Beds of Lesotho. *Zoological Journal of the Linnean Society*, **55**, 151–175.

THULBORN, R. A. 1992. Taxonomic characters of *Fabrosaurus australis*, an ornithischian dinosaur from the lower Jurassic of Southern Africa. *Geobios*, **25**, 283–292.

TIXERONT, M. 1973. Lithostratigraphie et minéralisations cuprifères et uranifères stratiformes syngénétiques et familières des formations détritiques Permo-triassiques du couloir d'Argana, Haut-Atlas occidental (Maroc). *Notes du Service Géologique du Maroc*, **33** (249), 147–177.

WEISHAMPEL, D. B. 1990. Dinosaurian distribution. 63–139. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria.* University of California Press, Berkeley, Los Angeles, Oxford, 733 pp.

—— DODSON, P. and OSMÓLSKA, H. 1990. *The Dinosauria.* University of California Press, Berkeley, Los Angeles, Oxford, 733 pp.

YOUNG, C. C. 1947. On *Lufengosaurus magnus* Young (sp. nov.) and additional finds of *Lufengosaurus huenei* Young. *Palaeontologica Sinica*, **132** (new series C, 12) 1–53.

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